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ENERGETICS OF TOUCANS, A BARBET, AND A HORNBILL: IMPLICATIONS FOR AVIAN FRUGIVORY

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ABSTRACT.—Rate of oxygen consumption was measured in eight species of toucans, one barbet, and one hornbill to examine factors that influence their energy expenditures. Basal rate of metabolism in those species, supplemented with measurements from three woodpeckers and three mousebirds, is correlated with body mass and either food habits or climate: temperate acorn- and insect-eating species have basal rates that are ~70% greater than tropical fruit-eating species. The temperate, insect- or acorn-eating species are woodpeckers, so level of basal rate is also correlated with familial affiliation. The toucans, barbet, and hornbill have basal rates similar to those of frugivorous pigeons and bats, which collectively are low by avian standards. The effects of climate, food habits, and family affiliation on basal rates in endotherms are difficult to separate, given the restricted data set available. Earlier conclusions that the basal rates of birds greatly exceed those of mammals are confounded by character interactions that influence dependence of basal rate on body mass. The largest toucan showed a remarkable ability to reduce energy expenditure at low ambient temperatures without reducing core body temperature, possibly as a result of peripheral vasoconstriction. *Received 7 June 1999, accepted 16 April 2001.*

BIRDS HAVE BASAL rates of metabolism that vary with many factors, including body mass. They are described as having higher basal rates than mammals, with passerines having higher basal rates than other birds (Lasiewski and Dawson 1967, Aschoff and Pohl 1970), and they have a circadian rhythm in which the rate is highest, even when inactive, during the normal period of activity (Aschoff and Pohl 1970). A recent analysis by Reynolds and Lee (1996) argued that passerines do not have higher basal rates than other birds, a conclusion first suggested by Prinzinger and Hänssler (1980), although the data used by Reynolds and Lee were not stipulated and potentially included measurements that do not meet strict standards for basal rate (McNab 1997). Nevertheless, much interspecific variation is found in basal rate, even when body size, taxonomy, and time of day are taken into consideration. Although the extent to which that residual variation includes measurement error is unclear, the largest proportion is correlated with the natural history of the species studied. Thus, Weathers (1979) showed that latitude (and climate) has an effect on basal metabolic rate in birds; Ellis (1980, 1984) demonstrated that basal rate is correlated with plumage color in species exposed at low latitudes to high levels of solar radiation; McNab (1988a) suggested that the basal rate of birds is correlated with food habits; McNab and Bonaccorso (1995) showed that basal rate in insectivorous birds is correlated with foraging style; and McNab (2000) demonstrated that the basal rate of frugivorous pigeons in the South Pacific is correlated with island size.

Here I present data on temperature regulation and rate of metabolism of eight species of toucans that belong to five of the six genera, on one species of African ground-barbet (*Trachyphonus darnaudii*), and on Blyth's Hornbill (*Aceros plicatus*), a member of the palaeotropical family Bucerotidae. The toucan family Ramphastidae is limited in distribution to the Neotropics, which along with woodpeckers (Picidae), honeyguides (Indicatoridae), jacamars (Galbulidae), puffbirds (Bucconidae), and barbets (Capitonidae) constitute the order Piciformes. Recent analyses, however, have suggested that New World barbets constitute a subfamily (Capitoninae) of the Ramphastidae (Prum 1988), whereas African barbets are placed in the family Lybiidae and Asian barbets in the family Megalaimidae (Sibley and Ahlquist 1990).

Toucans are of special interest because of their commitment to frugivory (Remsen et al. 1993), although large species also opportunistically prey on birds and mammals (Skutch

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1983, Boinski 1987, Mitchell et al. 1991). Propensity for carnivory in some toucans is most marked in the highlands, which may compensate for a reduced fruit availability (Galetti et al. 2000). African ground-barbets feed on fruit and insects (Short and Horne 1980). Hornbills, traditionally placed in the order Coraciiformes, represent an ecotype convergent with toucans, large arboreal species, such as *A. plicatus,* being highly frugivorous (Kemp 1995).

These data permit an examination of effect of body size, food habits, behavior, and climate on energetics of tropical nonpasserine frugivores through a comparison of toucan energetics with those of the barbet, hornbill, and three mousebirds (Bartholomew and Trost 1970, Prinzinger et al. 1981, Prinzinger 1988). Toucans are also compared with woodpeckers (Kendeigh et al. 1977, Weathers et al. 1990), the only other piciforms that have had their energetics measured. In addition, I compare the energy expenditures of those frugivores with those of frugivorous pigeons (McNab 2000) and fruit bats belonging to the family Pteropodidae (Bonaccorso and McNab 1997, McNab and Armstrong 2001, McNab and Bonaccorso 2001).

METHODS

Birds.—I studied 10 species of birds. They were (1) D'Arnaud's Ground-Barbet (*Trachyphonus darnaudii;* one male and one female borrowed from the Lowry Park Zoo, Tampa, Florida), a species that occurs in East Africa from the Sudan to Tanzania in dry brush country. (2) Saffron Toucanet (*Baillonius bailloni;* one male and one female borrowed from the Central Florida Zoological Park, Lake Monroe, Florida) lives in the Atlantic rainforest of Brazil. (3) Groove-Billed Toucanet (*Aulacorhynchus sulcatus;* one male and one female studied at the Parque Ambiental y Zoológico Gustavo Rivera, Falcón, Venezuela) occurs in northern Colombia and Venezuela. (4) Emerald Toucanet (*Aulacorhynchus prasinus;* one male and one female borrowed from the Lowry Park Zoo) lives in southern Mexico and Central America south to Venezuela, Colombia, Ecuador, and Peru. (5) Spot-Billed Toucanet (*Selenidera maculirostris;* two males and one female borrowed from the Lowry Park Zoo) is found in Brazil south of the Amazon to northeast Argentina. (6) Black-Necked Araçari (*Pteroglossus aracari;* one male and one female studied at the Parque Ambiental y Zoológico Gustavo Rivera) lives from Venezuela and the Guianas south through southern Brazil. (7) Red-Breasted Toucan (*Ramphastos dicolorus;* one male and one female borrowed from Lowry Park Zoo) occurs in southeastern Brazil to Paraguay and northern Argentina. (8) Red-Billed Toucan (*Ramphastos tucanus;* one male and one female studied at the Parque Ambiental y Zoológico Gustavo Rivera) occurs principally in the tropical lowlands of South America north of the Amazon River. (9) Toco Toucan (*Ramphastos toco;* one male and one female borrowed from the Lowry Park Zoo) lives in South America from the Guianas and Brazil south to Paraguay and northern Argentina. (10) Blyth's Hornbill (*Aceros plicatus;* one male and one female, semicaptives studied at Christensen Research Institute, Madang, Papua New Guinea) inhabits Burma east to Sulawesi, New Guinea, the Bismarck Archipelago, and the Solomon Islands, although some of its distribution east of New Guinea may be due to human transport (D. W. Steadman pers. comm.).

Some captive individuals used in this study were caught in the wild, whereas others were the product of captive breeding. They ate a variety of fruits with protein and vitamin supplements and lived under the local natural photoperiod and temperature regimes. Measurements in Venezuela occurred in August and December, in Papua New Guinea in July, and in Florida in fall or spring.

Experimental techniques.—Measurements of rate of metabolism, as oxygen consumption, occurred in an open system. Room air was sucked through a chamber, the size of which varied with the size of a bird: a 329 L hollow-walled chamber was connected to a thermoregulated water bath; a 2 and a 44 L chamber, the temperatures of which were regulated by placing the chamber into the hollow-walled chamber; or a 15 and a 27 L chamber was placed a temperature-controlled refrigerator. The barbet was measured in a 2 L chamber, most toucans in the 15 or 44 L chamber, and the Toco Toucan both in the 44 and 329 L chambers. Hornbills were confined in the 27 L chamber during measurements. After being removed from the chamber, air was sequentially scrubbed of CO_2 (by indicating soda lime) and water (by indicating silica gel). The air stream then went to a flowmeter and to an Applied Electrochemistry S3A-II Oxygen Analyzer, the outputs of which went to a stripchart recorder. The flow rates varied with chamber size: flow rates were 0.6 to 0.9 L min^{-1} in the 2 L chamber, 1.0 to 1.5 L min^{-1} in the 15 L chamber, 4.1 to 6.6 L min^{-1} in the 27 L chamber, 2.1 to 2.7 L min^{-1} in the 44 L chamber, and 4.5 to 9.0 L min^{-1} in the 329 L chamber. Those rates were high enough to ensure an adequate mixture of air in the chamber, as was demonstrated by independence of the calculated rate of metabolism from flow rate.

To minimize the influence of activity, minimal rates of metabolism that lasted ≥ 2 min were used; individual runs usually lasted 2–3 h. The experiments reported here represented a total of 1,572 h of measurements; usually two experiments were run at the same time. The cloacal temperature and body mass of the birds were measured at the terminus of each experiment, preferentially when rate of metabolism was minimal to determine whether low rates reflect low body temperatures. The range in ambient temperature used permitted the zone of thermoneutrality, basal rate of metabolism, and minimal thermal conductance to be estimated. Measurements in most species were made both at night and during the day to determine whether rate of metabolism showed a circadian rhythm.

Thermal conductance was estimated from $C = \dot{V}_{O_2}/\Delta T$, where C is thermal conductance (cm^3 O$_2$ g^{-1} h^{-1} °C^{-1}), $\dot{V}_{O_2}$ is rate of metabolism (cm^3 O$_2$ g^{-1} h^{-1}), and ΔT is the temperature differential between body and ambient (McNab 1980). Thermal conductances at temperatures below thermoneutrality often were not constant: conductances tend to decrease with a fall in ambient temperature. Under those circumstances, similar conductances were grouped together over a range in ambient temperatures. Mean conductances were placed in the figures as the slope of a curve that extrapolated to the mean body temperature in the sample when rate of metabolism equaled zero, as required by the Scholander-Irving model (Scholander et al. 1950). Thus, in *Trachyphonus*, three mean thermal condutances were calculated, one that corresponded to the lower limit of thermoneutrality, one that represented minimal thermal conductance, and one that was intermediate (Fig. 1A). All measurements of metabolism were corrected to standard dry temperature and pressure.

Various authors (Nickerson et al. 1989) have advocated a mathematical technique to determine an intersection between two curves, which potentially could be used to determine the lower limit of thermoneutrality and the slope of the curve below thermoneutrality. The difficulties with its application to metabolism data are that (1) the lower limit of thermoneutrality does not correspond to the thermal conductance at lower temperatures (*B. bailloni*); (2) thermal conductance decreases with a fall in ambient temperature (*T. darnaudii, A. prasinus, R. dicolorus, R. tucanus, R. toco*), which means that the slope of the pooled fitted curve below thermoneutrality is not thermal conductance (McNab 1980); or (3) the rate of metabolism below thermoneutrality decreases (*R. toco*). The technique used by Yeager and Ultsch (1989) to estimate intersection of two curves depends on their linearity, which is often not the case for metabolism at temperatures below thermoneutrality. Any error involved in estimating the lower limit of thermoneutrality by other than a mathematical technique is not greater by more than 1–2°C, which has no appreciable effect on the conclusions stated here.

Statistics.—To alleviate the potential problem of having only a few individuals of a species available, an *F*-test was used to determine whether the interindividual variation in the rate of metabolism in the zone of thermoneutrality, an estimate of the basal rate, was significant. If not, all measurements were pooled and used in calculation of the mean and SE (n = number of measurements). An examination of data shows (see below) that no significant difference existed in basal rate among individuals in 8 of the 10 species. The range in individual basal rates, expressed relative to values expected from body mass, within a species was ≤8%, and pooled estimates of basal rates are within 1% of those obtained by averaging means of the individual performances. The two exceptions reflect either a noticeable sexual dimorphism in body mass (*A. plicatus*) or possibly a sexually based difference in behavior (*S. maculirostris*). A further complication occurs when no difference among individuals is found in mass-specific basal rate, but a difference is found in body mass, which means that a difference occurs in total basal rate (*R. dicolorus*). In those cases, a species mean was derived from averaging individual means.

I used an ANCOVA package (Super ANOVA; Abacus Concepts, Berkeley, California) to determine whether basal rate of metabolism or minimal thermal conductance was correlated with body mass, climate, food habits, and family affiliation in the species studied here supplemented with data from the literature on mousebirds and woodpeckers. To facilitate those analyses, basal rate and minimal conductance (dependent variables) were entered in separate analyses with total units as logarithms, as was body mass, to convert these power functions into linear equations.

When classifying species into ecological or behavioral categories, difficulties are encountered because those aspects of the life of species are more complex than simple categories will reflect. However, if the categories reflect precisely the diversity in habits, most statistical cells will contain only one species. Furthermore, seasonal and geographical variations in food habits contributes to complexity of classification. The best that can be done is to recognize broad trophic or climatic categories as an approximation, which can be attained by lumping categories that do not show statistically significant differences and rerunning the statistical analyses. In these analyses, the results are presented after all insignificant factors are discarded. Statistical significance was ≤0.05.

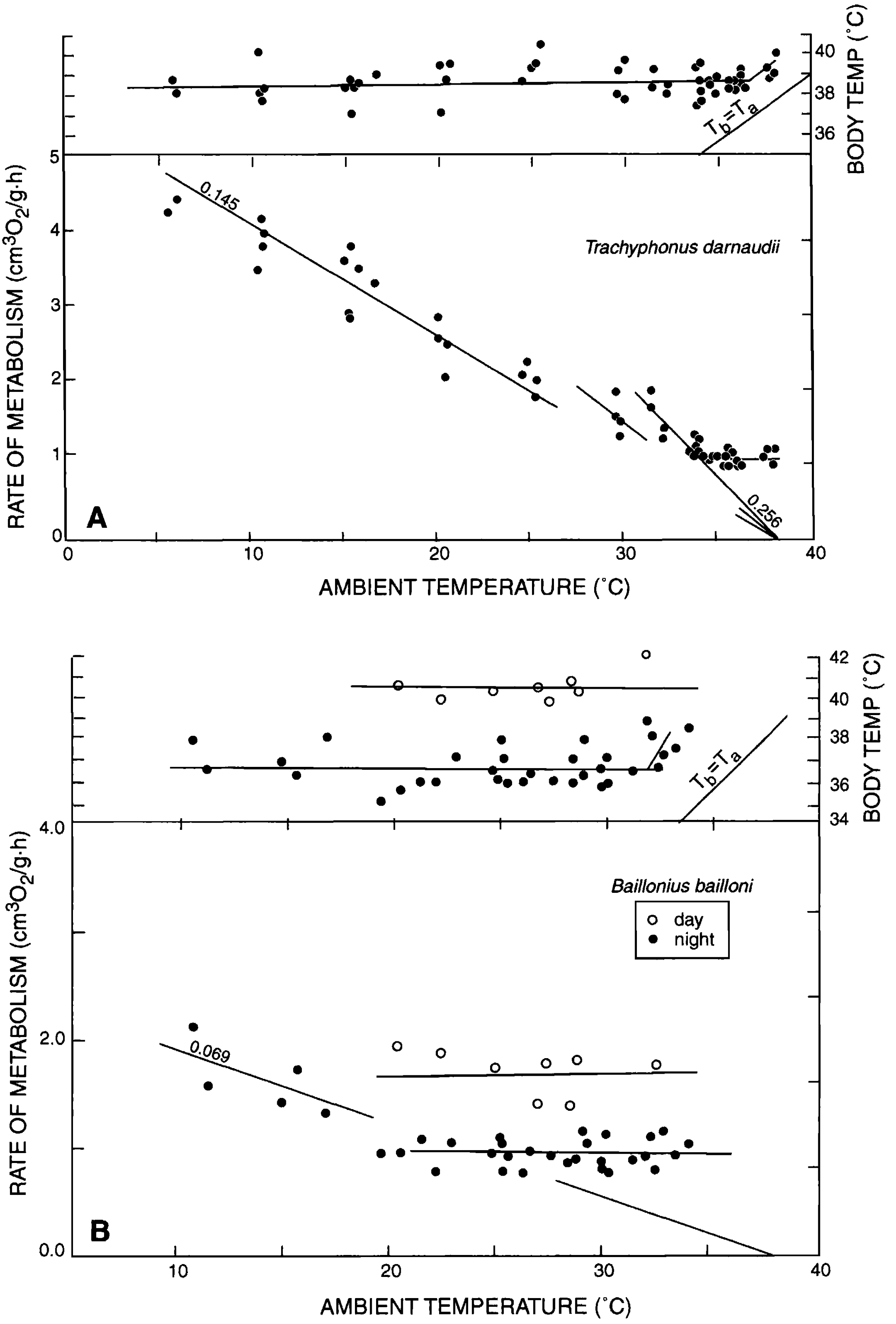
RESULTS

Trachyphonus darnaudii.—The two D'Arnaud's Ground-Barbets used in this study weighed 36.6 ± 0.12 g. All measurements (n = 50) were made at night. The range of thermoneutrality was narrow, only from 35 to 38°C (Fig. 1A), which reflects its small size. Within that range, basal rate of metabolism equaled 1.07 ± 0.023 cm^3 O$_2$ g^{-1} h^{-1} (n = 16), which is 71% of the basal rate expected from the curve for nonpasserines (Aschoff and Pohl 1970). Basal rate did not differ ($F = 2.00$, df = 1 and 14, $P = 0.18$) between those individuals, their means being 69 ($n = 8$) and 73% ($n = 8$) of the values expected from body mass, the mean of which is 71%. Body temperature at ambient temperatures below 35°C equaled 38.3 ± 0.15°C ($n = 38$). The increase in rate of metabolism at temperatures below thermoneutrality did not conform to one simple relationship (Fig. 1A and above); the lower limit of thermoneutrality was set by a conductance equal to 0.278 ± 0.0134 cm^3 O$_2$ g^{-1} h^{-1} °C^{-1} ($n = 10$), whereas minimal thermal conductance at ambient temperatures between 5 and 25°C was 0.145 ± 0.0039 cm^3 O$_2$ g^{-1} h^{-1} °C^{-1} ($n = 20$), which is 103% of the value expected from the curve described by Lasiewski et al. (1967) and 57% of the conductance that defines the lower limit of thermoneutrality. Minimal conductances did not differ ($F = 1.27$, df = 1 and 18, $P = 0.28$) between the two individuals.

Baillonius bailloni.—Two Saffron Toucanets were measured, a male that weighed 136.2 ± 0.79 g ($n = 25$) and his daughter that weighed 129.8 ± 0.81 g ($n = 22$). The zone of thermoneutrality extended from 19 to 34°C (Fig. 1B). The basal rate in the male was 0.906 ± 0.0297 cm^3 O$_2$ g^{-1} h^{-1} ($n = 15$), which is 85% of the value expected from mass, whereas the female had a basal rate equal to 0.989 ± 0.0311 cm^3 O$_2$ g^{-1} h^{-1} ($n = 13$), which is 92% of the expected value (mean of the individuals = 89%). Within this zone, no difference ($F = 3.33$, df = 1 and 26, $P < 0.08$) existed between those individuals in the mass-specific basal rates. The mean basal rate of this toucanet was 0.948 cm^3 O$_2$ g^{-1} h^{-1}, which is 89% of the value expected from a mean mass of 133.0 g. In spite of the difference in body mass, no difference was found ($F = 0.42$, df = 1 and 26, $P = 0.52$) between the total basal rates of the male (123.9 ± 4.29 cm^3 O$_2$ h^{-1}) and the female (128.0 ± 4.61 cm^3 O$_2$ h^{-1}), the mean being 126.0 cm^3 O$_2$ h^{-1}. During daytime, the rate of metabolism in thermoneutrality was almost twice the night rate: 1.71 ± 0.072 cm^3 O$_2$ g^{-1} h^{-1} °C^{-1} ($n = 8$). Body temperature during nighttime equaled 36.7 ± 0.15°C ($n = 31$) at ambient temperatures below 31°C, the female having a slightly higher body temperature (37.2 ± 0.21°C [$n = 12$]) than the male (36.5 ± 0.17°C [$n = 19$]). During the day, body temperature equaled 40.4 ± 0.15°C ($n = 8$). At ambient temperatures below 17°C, thermal conductance equaled 0.069 ± 0.0044 cm^3 O$_2$ g^{-1} h^{-1} °C^{-1} ($n = 5$), which is 94% of the value expected from the average mass. It did not differ ($F = 0.26$, df = 1 and 3, $P = 0.64$) between the two toucanets.

Aulacorhynchus sulcatus.—The two Groove-Billed Toucanets had a mean mass that was 131.7 ± 2.18 g ($n = 29$). Thermoneutrality extended from 23 to 31°C (Fig. 2A), within which basal rate of metabolism equaled 0.923 ± 0.0624 cm^3 O$_2$ g^{-1} h^{-1} ($n = 7$), which is 86% of the value expected from mass. Basal rate did not differ ($F = 0.45$, df = 1 and 5, $P = 0.84$) between the two individuals, which equaled 87 ($n = 5$) and 84% ($n = 2$) of the expected values (mean = 86%). Three daytime measurements in thermoneutrality were higher (1.32 ± 0.023 cm^3 O$_2$ g^{-1} h^{-1}). Body temperature at ambient temperatures between 15 and 25°C was 38.8 ± 0.38°C ($n = 7$) at night and 40.7 ± 0.28°C ($n = 8$) during the day. Mean thermal conductance at night was 0.059 ± 0.0032 cm^3 O$_2$ g^{-1} h^{-1} °C^{-1} ($n = 7$), which is 80% of the value expected from mass, whereas conductance during the day was 0.066 ± 0.0032 cm^3 O$_2$ g^{-1} h^{-1} °C^{-1} ($n = 5$), some of the difference reflecting a difference in body temperature, 38.4 versus 40.4°C, respectively. The nocturnal conductance did not differ ($F = 0.18$, df = 1 and 5, $P = 0.69$) between the two individuals.

Aulacorhynchus prasinus.—The two Emerald Toucanets had a mean body mass equal to 174.7 ± 1.47 g ($n = 56$). The zone of thermoneutrality extended from 23 to 34°C (Fig. 2B). Basal rate of metabolism was 0.854 ± 0.0186 cm^3 O$_2$ g^{-1} h^{-1} ($n = 20$), or 86% of the value expected from mass. No difference ($F = 2.51$, df = 1 and 18, $P = 0.13$) existed in basal rate between the two individuals studied, which equaled 83 ($n = 10$) and 89% ($n = 10$) of the values expected from mass (mean = 86%). The daytime rate of metabolism in thermoneutrality was 1.17 ± 0.073 cm^3 O$_2$ g^{-1} h^{-1} ($n = 5$). Body temperature at night was independent of ambient temperature below 31°C and equaled 38.1 ± 0.07°C ($n = 41$); during the day it was higher: 40.5 ± 0.30°C ($n = 7$). Two thermal conductances are described for the Emerald Toucanet, one that defined the lower limit of thermoneutrality, 0.057 ± 0.0024 cm^3 O$_2$ g^{-1} h^{-1} °C^{-1} ($n = 10$), and the other that was minimal, 0.046 ± 0.0010 cm^3 O$_2$ g^{-1} h^{-1} °C^{-1} ($n = 13$), which is 79% of the value expected


BODY TEMP (˚C)
40
38
36
$T_b=T_a$
5
4
3
2
1
0
RATE OF METABOLISM ($cm^3O_2/g\cdot h$)
0.145
Trachyphonus darnaudii
0.256
A
0
10
20
30
40
AMBIENT TEMPERATURE (˚C)
42
40
38
36
34
BODY TEMP (˚C)
$T_b=T_a$
4.0
2.0
0.0
RATE OF METABOLISM ($cm^3O_2/g\cdot h$)
Baillonius bailloni
○ day
● night
0.069
B
10
20
30
40
AMBIENT TEMPERATURE (˚C)

from mass. Minimal conductance did not differ ($F = 0.10$, df = 1 and 11, $P = 0.76$) between those two toucanets.

Selenidera maculirostris.—The female Spot-Billed Toucanet had a mean body mass equal to 130.5 ± 1.51 g ($n = 13$), whereas the two males had masses equal to 142.7 ± 0.63 g ($n = 13$) and 144.5 ± 2.26 g ($n = 13$). The zone of thermoneutrality extended from 24 to 34°C (Fig. 3A). Within that range, the mass-specific basal rate was correlated ($F = 15.92$, df = 1 and 17, $P < 0.001$) with the sex of the individual: it was 1.35 ± 0.020 $\text{cm}^3\ \text{O}_2\ \text{g}^{-1}\ \text{h}^{-1}$ ($n = 14$) in the two males, which did not differ from each other ($F = 1.37$, df = 1 and 12, $P = 0.26$), and 1.51 ± 0.046 $\text{cm}^3\ \text{O}_2\ \text{g}^{-1}\ \text{h}^{-1}$ ($n = 5$) in the female. The two males had rates that were 127 ($n = 7$) and 130% ($n = 7$) of values expected from mass and that of the female was 141% of the expected rate. If those are basal rates, they are by far the highest, corrected for body mass, measured in toucans. Even after measurements with overt activity were excluded, rate of metabolism in thermoneutrality during the day was higher than at night: 1.69 ± 0.007 $\text{cm}^3\ \text{O}_2\ \text{g}^{-1}\ \text{h}^{-1}$ ($n = 4$).

Nocturnal body temperatures in that species were highly variable, especially within the zone of thermoneutrality (Fig. 3A): at ambient temperatures between 17 and 35°C, body temperature was bimodally distributed, either equaling 38.6 ± 0.16°C ($n = 12$), which was always associated with a lower rate of metabolism, or 41.1 ± 0.10 °C ($n = 23$), which was associated either with a higher or a lower rate of metabolism. At ambient temperatures <15°C, nocturnal body temperature was 41.2 ± 0.26 °C ($n = 6$) (Fig. 3A). The higher nocturnal body temperatures were similar to diurnal body temperatures, which equaled 41.1 ± 0.15°C ($n = 4$). Thermal conductance in the female was 0.095 ± 0.0019 $\text{cm}^3\ \text{O}_2\ \text{g}^{-1}\ \text{h}^{-1}\ {}^\circ\text{C}^{-1}$ ($n = 4$), which is 128% of the value expected from mass, whereas in the males it was 0.084 ± 0.0040 $\text{cm}^3\ \text{O}_2\ \text{g}^{-1}\ \text{h}^{-1}\ {}^\circ\text{C}^{-1}$ ($n = 8$), which is 118% of the expected value (Fig. 3A). The data from this species do not give an internally consistent picture of its energetics.

Pteroglossus aracari.—The two Black-Necked Araçaris had a mean mass of 200.7 ± 2.04 g ($n = 33$). Thermoneutrality extended from 29 through 35°C (Fig. 3B). Within that temperature range, basal rate equaled 0.794 ± 0.054 $\text{cm}^3\ \text{O}_2\ \text{g}^{-1}\ \text{h}^{-1}$ ($n = 11$), which is 83% of the value expected from mass; no difference ($F = 0.13$, df = 1 and 9, $P = 0.73$) was found in between the two individuals, which had basal rates equal to 82 ($n = 6$) and 85% ($n = 5$) of the values expected from mass (mean = 84%). During the day, rate of metabolism at those temperatures was 1.20 ± 0.103 $\text{cm}^3\ \text{O}_2\ \text{g}^{-1}\ \text{h}^{-1}$ ($n = 3$), which was different ($F = 12.00$, df = 1 and 12, $P = 0.005$) from nocturnal measurements. Body temperature was independent of ambient temperatures between 11 and 35°C: at night it was 38.0 ± 0.17°C ($n = 17$), whereas during the day it was appreciably higher, 40.9 ± 0.28°C ($n = 13$). Thermal conductance was highly variable, with no difference between day and night ($F = 2.89$, df = 1 and 15, $P = 0.11$) or between the two individuals ($F = 2.16$, df = 1 and 5, $P = 0.20$); the mean equaled 0.089 ± 0.0055 $\text{cm}^3\ \text{O}_2\ \text{g}^{-1}\ \text{h}^{-1}\ {}^\circ\text{C}^{-1}$ ($n = 17$), which is 148% of value expected from body mass.

Ramphastos dicolorus.—The Red-Breasted Toucan was represented by two individuals, a male, whose mass was 356.7 ± 2.08 g ($n = 22$), and a female, whose mass was 301.1 ± 0.52 g ($n = 22$). All measurements were made at night. The zone of thermoneutrality extended from 20 to 34°C (Fig. 4A). Within that range no difference ($F = 0.17$, df = 1 and 25, $P = 0.69$) in mass-specific basal rate was seen between the two individuals in spite of difference in their masses; mean basal rate was 0.689 ± 0.0229 $\text{cm}^3\ \text{O}_2\ \text{g}^{-1}\ \text{h}^{-1}$ ($n = 27$), which is 82% of the value expected from an average mass of 328.9 g, or 83% of the value expected from the male's mass and 81% of the value expected from the female's mass. Those data mean that the male had a higher ($F = 5.29$, df = 1 and 25, $P = 0.03$) total rate (242.9

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FIG. 1. Body temperature and rate of metabolism as a function of ambient temperature in (A) two D'arnaud's Ground-Barbets (*Trachyphonus darnaudii*) and (B) two Saffron Toucanets (*Baillonius bailloni*). At ambient temperatures below thermoneutrality, thermal conductance equals the slope of the fitted curves, the value of which is indicated by a decimal fraction. All measurements in the ground-barbet were made at night.

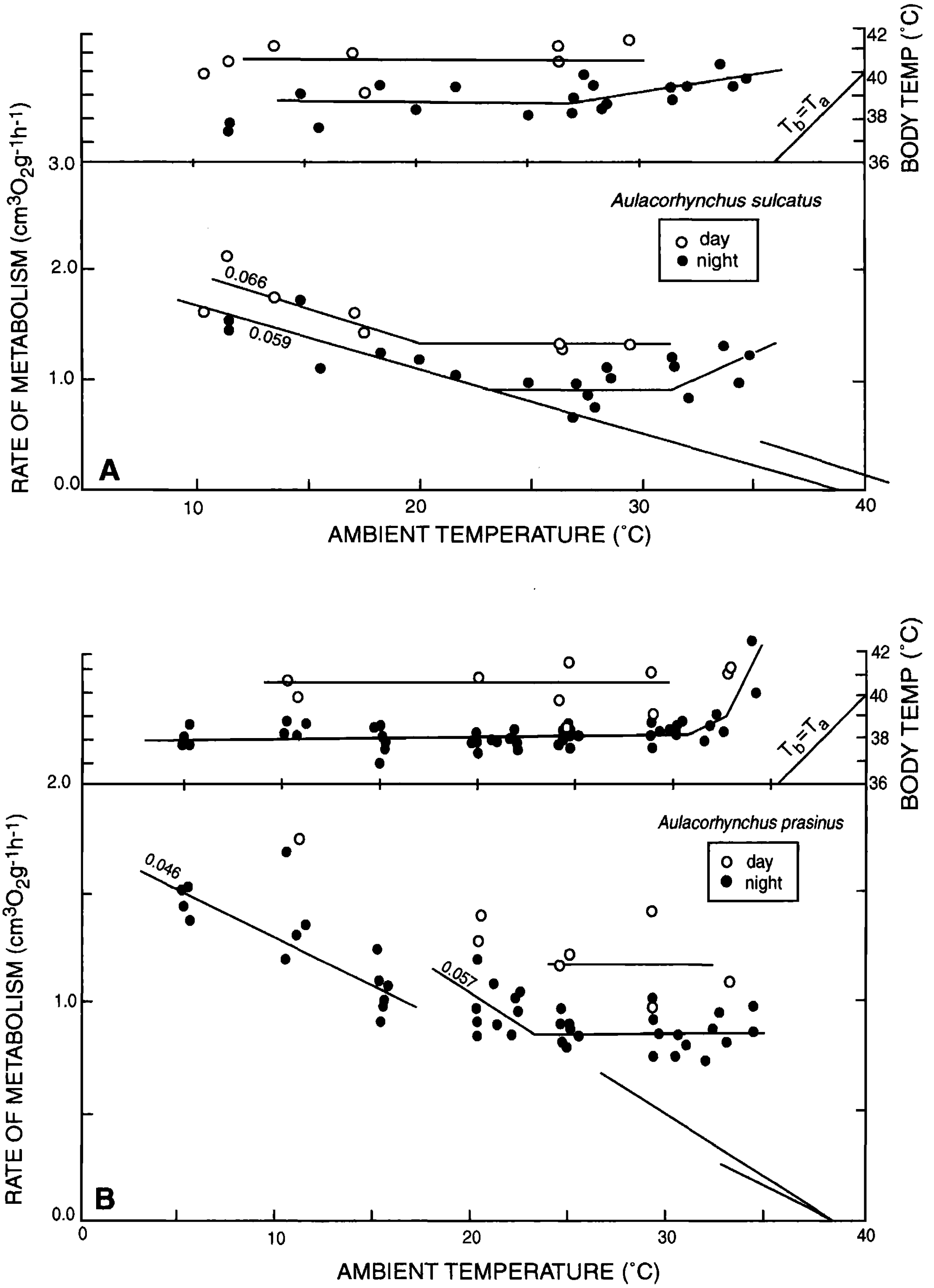


FIG. 2. Body temperature and rate of metabolism as a function of ambient temperature in (A) two Groove-Billed Toucanets (*Aulacorhynchus sulcatus*) and (B) two Emerald Toucanets (*Aulacorhynchus prasinus*).

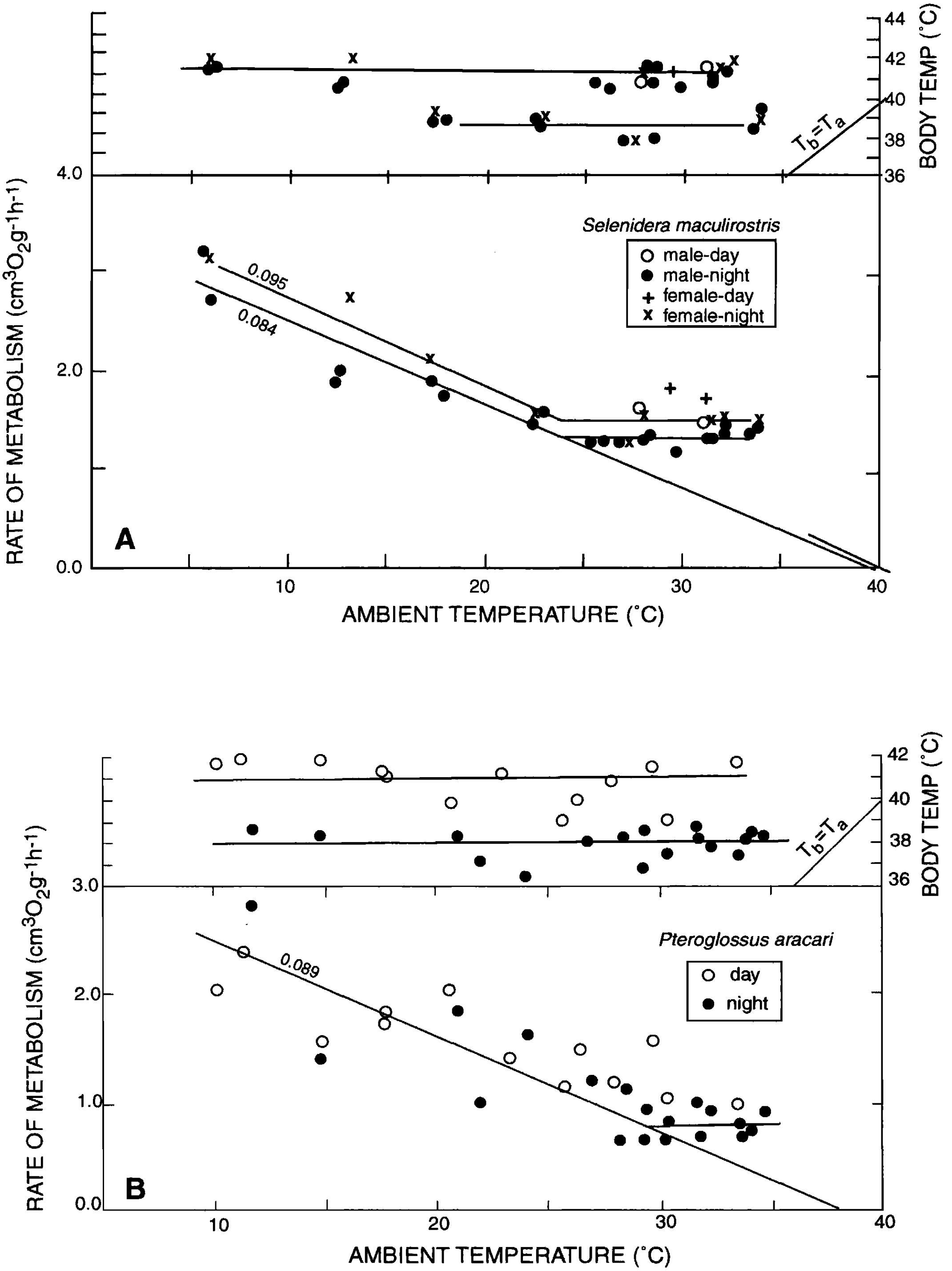
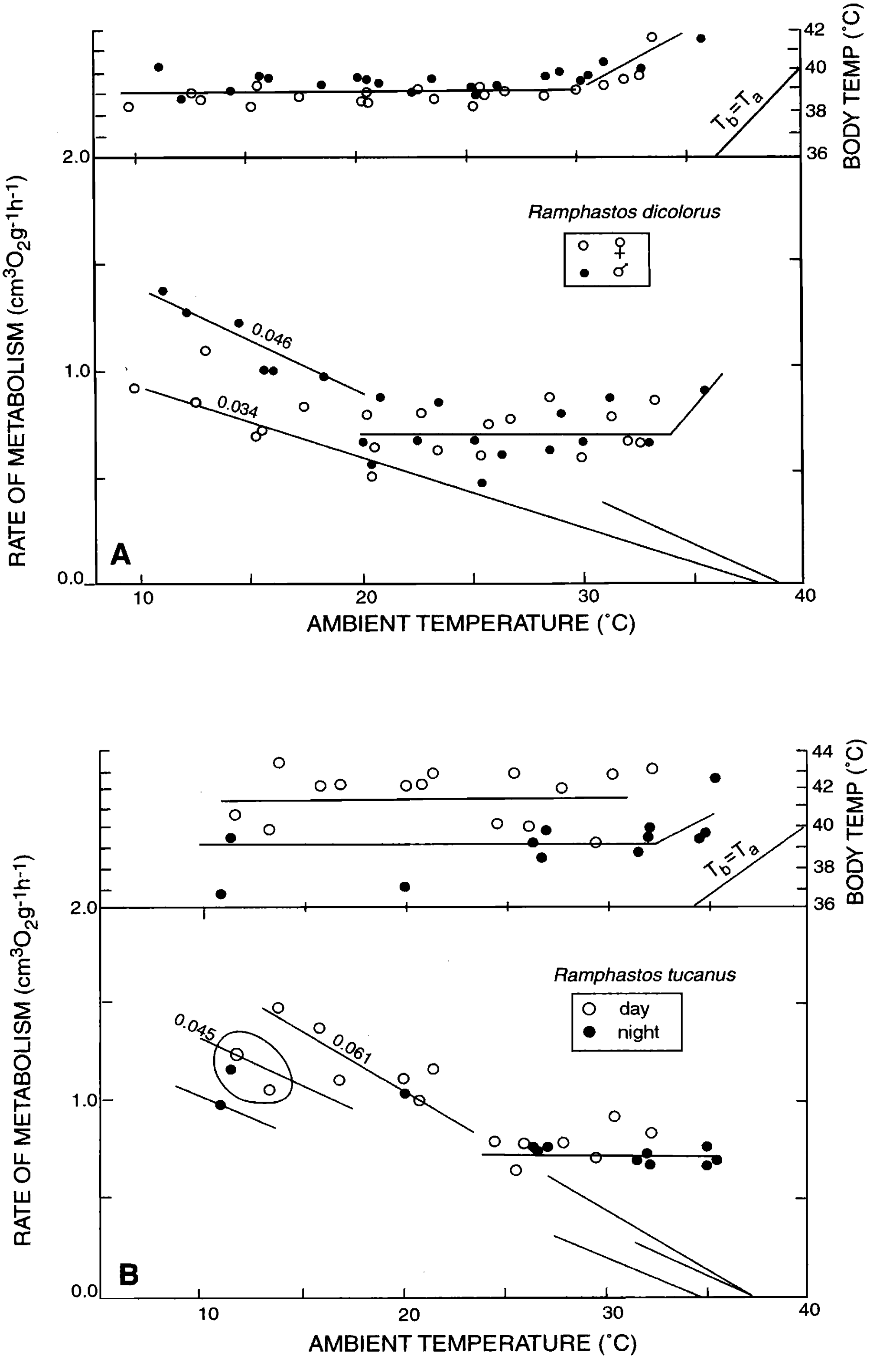


FIG. 3. Body temperature and rate of metabolism as a function of ambient temperature in (A) three Spot-Billed Toucanets (*Selenidera maculirostris*) and (B) two Black-Necked Araçaris (*Pteroglossus aracari*).


BODY TEMP (°C)
42
40
38
36
2.0
T_b=T_a
Ramphastos dicolorus
○ ♀
● ♂
0.046
0.034
1.0
0.0
RATE OF METABOLISM (cm³O₂g⁻¹h⁻¹)
A
10
20
30
40
AMBIENT TEMPERATURE (°C)
BODY TEMP (°C)
44
42
40
38
36
2.0
T_b=T_a
Ramphastos tucanus
○ day
● night
0.045
0.061
1.0
0.0
RATE OF METABOLISM (cm³O₂g⁻¹h⁻¹)
B
10
20
30
40
AMBIENT TEMPERATURE (°C)

± 10.34 cm^3 O_2 h^{-1}) than the female (209.9 ± 9.97 cm^3 O_2 h^{-1}), which raises the question of which rates are ecologically and evolutionarily "relevant," total or mass-specific (see McNab 1999). The mean total basal rate in this species was 226.6 ± 10.2 cm^3 O_2 h^{-1}.

Body temperature at ambient temperatures from 9 to 30°C equaled 39.2 ± 0.09°C ($n = 32$). Thermal conductance in the male was higher ($F = 34.81$, df = 1 and 12, $P \leq 0.001$) than found in the female (Fig. 4A) 0.046 ± 0.002 cm^3 O_2 g^{-1} h^{-1} $°C^{-1}$ ($n = 6$), which is 102% of the value expected from the male's mass, and 0.034 ± 0.002 cm^3 O_2 g^{-1} h^{-1} $°C^{-1}$ ($n = 6$), or 69% of the value expected from the female's mass. If a unified conductance is preferred, it would be 0.041 cm^3 O_2 g^{-1} h^{-1} $°C^{-1}$, which is 87% of the value expected from a 328.9 g mass.

Ramphastos tucanus.—The two Red-Billed Toucans had a mean mass equal to 420.3 ± 8.27 g ($n = 24$). The zone of thermoneutrality extended from 25 to 35°C (Fig. 4B). Within that range, the basal rate, measured at night, equaled 0.729 ± 0.0154 cm^3 O_2 g^{-1} h^{-1} ($n = 9$), which is 93% of the value expected from mass. No difference ($F = 1.24$, df = 1 and 7, $P = 0.30$) was found in basal rate between the two individuals, which had basal rates equal to 92 ($n = 6$) and 96% ($n = 3$) of the expected values (mean = 94%). During the day, rate of metabolism in thermoneutrality was somewhat higher: 0.780 ± 0.0379 cm^3 O_2 g^{-1} h^{-1} ($n = 7$). Body temperature at ambient temperatures between 10 and 33°C was higher during the day (39.6 ± 0.32°C [$n = 15$]) than at night (36.8 ± 0.41°C [$n = 9$]; Fig. 4B). Conductance that corresponded to the lower limit of thermoneutrality was 0.061 ± 0.0034 cm^3 O_2 g^{-1} h^{-1} $°C^{-1}$ ($n = 6$). At ambient temperatures <17°C, thermal conductance decreased to 0.045 ± 0.0009 cm^3 O_2 g^{-1} h^{-1} $°C^{-1}$ ($n = 3$), which is 101% of the expected value and 74% of the conductance that defines the lower limit of thermoneutrality. A similar value, 0.042 cm^3 O_2 g^{-1} h^{-1} $°C^{-1}$, was measured at 11°C in association with a low body temperature (34.6°C).

Ramphastos toco.—Of two Toco Toucans, the male had a mean mass equal to 634.8 ± 1.00 g ($n = 31$) and the female had a mass equal to 527.6 ± 1.00 g ($n = 30$). Thermoneutrality extended from 17 to 34°C (Fig. 5A). Within that region, rate of metabolism was quite variable, but because all measurements were made at night, variability was not due to a circadian rhythm. One factor that contributed to the variation was that some measurements were made in a 44 L chamber and others in a 329 L chamber. The pooled rate measured in the large chamber was 0.750 ± 0.022 cm^3 O_2 g^{-1} h^{-1} ($n = 19$), which is 105% of the rate expected from a mean mass of 581.2 g. The mass-specific rate in the male was 0.707 ± 0.026 cm^3 O_2 g^{-1} h^{-1} ($n = 10$), which is 101% of the expected value, and did not differ ($F = 3.69$, df = 1 and 17, $P = 0.07$) from that in the female, which was 0.798 ± 0.040 cm^3 O_2 g^{-1} h^{-1} ($n = 9$), or 108% of the expected value. Total rate of metabolism also did not differ ($F = 1.09$, df = 1 and 17, $P = 0.31$) between the individuals, the mean of which is 434.9 ± 19.1 cm^3 O_2 h^{-1}. The rate measured in the smaller chamber was higher ($F = 15.00$, df = 1 and 36, $P = 0.0004$) than that measured in the larger chamber: 0.873 ± 0.022 cm^3 O_2 g^{-1} h^{-1} ($n = 19$), which is 122% of the expected rate. When those toucans were enclosed in the smaller chamber, they appeared to show much anxiety; the best estimate of basal rate therefore was measured in the large chamber. Body temperature at ambient temperatures between 0 and 32°C also reflected chamber size, although, surprisingly, body temperature was slightly lower ($F = 23.44$, df = 1 and 56, $P \leq 0.0001$) in the smaller chamber: 38.6 ± 0.08°C ($n = 29$) versus 39.1 ± 0.08°C ($n = 28$).

Chamber size had a qualitative effect on rate of metabolism at temperatures below thermoneutrality (Fig. 5A). When Toco Toucans were confined in the smaller chamber at ambient

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FIG. 4. Body temperature and rate of metabolism as a function of ambient temperature in (A) two Red-Breasted Toucans (*Ramphastos dicolorus*) and (B) two Red-Billed Toucans (*Ramphastos tucanus*). Circled points in the case of *R. tucanus* indicate rates that were associated with an intermediate thermal conductance. All measurements in *R. discolorus* were made at night; no difference was found in rate of metabolism between the male and female in thermoneutrality, but a marked difference was found at lower ambient temperatures (see text).

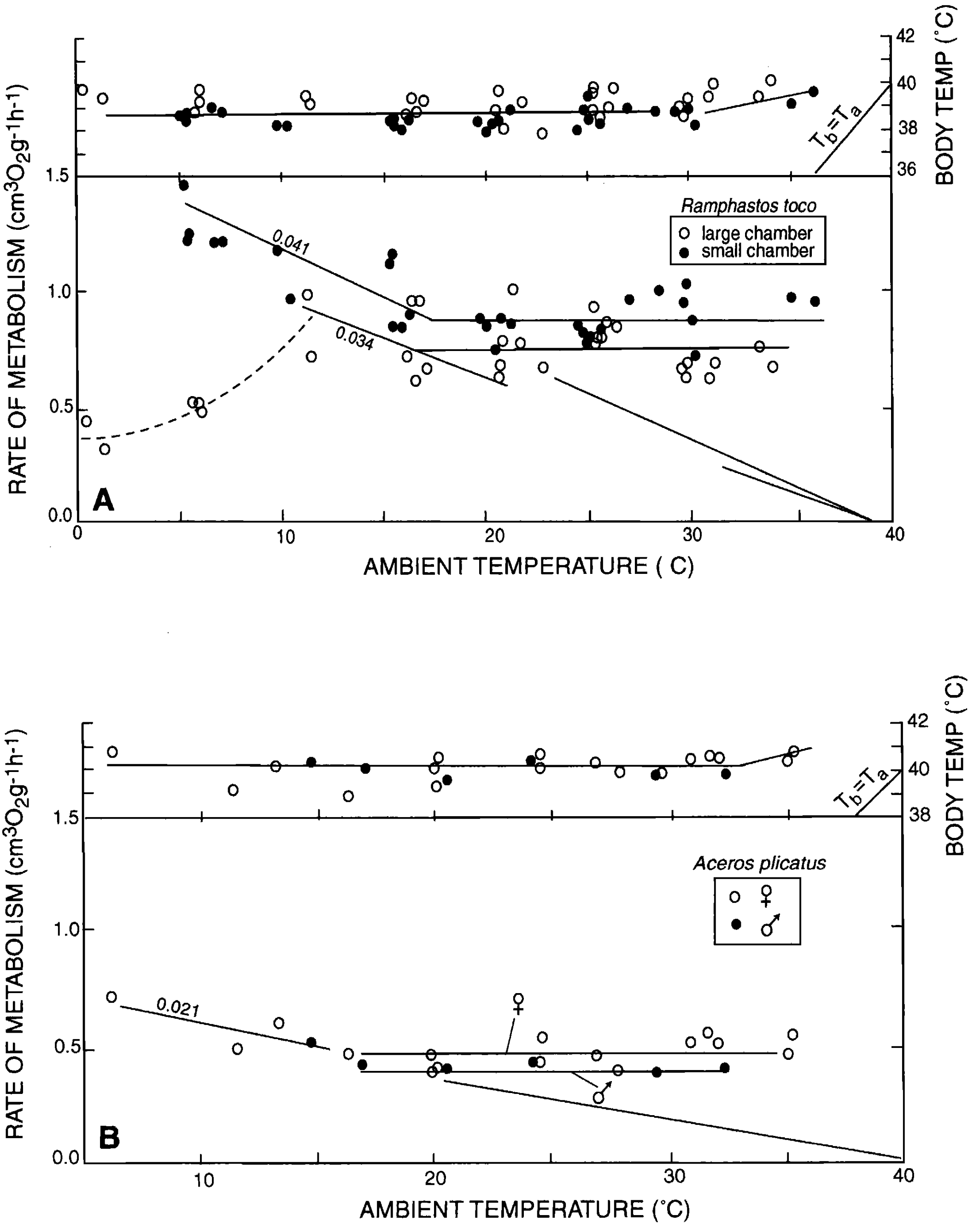

FIG. 5. Body temperature and rate of metabolism as a function of ambient temperature in (A) two Toco Toucans (*Ramphastos toco*) and (B) two Blyth's Hornbills (*Aceros plicatus*). All measurements in those species were made at night.

temperatures between 5 and 17°C, thermal conductance equaled 0.041 ± 0.0014 $cm^3 O_2 g^{-1} h^{-1} °C^{-1}$ ($n = 12$), which is 116% of the value expected from the mean mass; the two individuals showed no difference in that thermal conductance ($F = 0.05$, df = 1 and 10, $P = 0.83$). In the larger chamber at temperatures between 12 and 17°C, rate of metabolism conformed to a conductance equal to 0.034 ± 0.0026 $cm^3 O_2 g^{-1} h^{-1} °C^{-1}$ ($n = 7$), which is 96% of the expected value; no difference ($F = 0.64$, df = 1 and 5, $P = 0.46$) was found between the two individuals. At lower ambient temperatures, however, rate of metabolism fell without any decrease in core body temperature when toucans were confined in the large chamber (Fig. 5A). The decrease in rate of metabolism at low temperatures reflected a radical reduction in thermal conductance: at 0.8°C, thermal conductance was approximately equal to 0.010 $cm^3 O_2 g^{-1} h^{-1} °C^{-1}$ ($n = 2$), which is only 28% of the value expected from mass. The response to low ambient temperatures was reversed by shifting those toucans from one chamber to the other, and then restored to the original value by returning the toucan to the original chamber, so the response of that toucan to low ambient temperatures reflected chamber size.

Aceros plicatus.—Of the two Blyth's Hornbills studied here, the female weighed 1,597.4 ± 13.69 g ($n = 16$) and the male 1,965.8 ± 35.91 g ($n = 6$). All measurements were made at night. Thermoneutrality extended from 35 to 16°C (Fig. 5B), or possibly as low as 12°C in the female. Within this zone the basal rate of the female was 0.495 ± 0.0161 $cm^3 O_2 g^{-1} h^{-1}$ ($n = 13$), which is 91% of the expected value, and is greater ($F = 5.72$, df = 1 and 16, $P = 0.03$) than that of the male, which was 0.430 ± 0.0090 $cm^3 O_2 g^{-1} h^{-1}$ ($n = 5$), or 83% of the expected value. Therefore, in spite of a larger mass, the total basal rate in the male (838.7 ± 39.8 $cm^3 O_2 h^{-1}$) was not different ($F = 1.08$, df = 1 and 16, $P = 0.31$) from that of the female (789.9 ± 24.7 $cm^3 O_2 h^{-1}$), the mean of which is 814.3 ± 28.9 $cm^3 O_2 h^{-1}$. For interspecific comparisons, the mean basal rate would be 0.463 $cm^3 O_2 g^{-1} h^{-1}$, which is 87% of the rate expected from the mean mass of 1,781.6 g. Body temperature was 40.1 ± 0.11°C ($n = 21$) at ambient temperatures between 6 and 33°C. The thermal conductance that defined the lower limit of thermoneutrality equaled 0.021 ± 0.0009 $cm^3 O_2 g^{-1} h^{-1} °C^{-1}$ ($n = 4$), which is 104% of the value expected from the mean mass.

DISCUSSION

An examination of the variation in the standard energetics of toucans and other nonpasserine frugivores throws some light on factors that influence basal rate of metabolism and thermal conductance in those species. Those factors potentially include body size, food habits, climate, and taxonomic affiliation.

The response of some species to experimental procedures complicates analysis of their energetics. That was most apparent in two species contained in this study. *Selenidera maculirostris* showed a bimodal distribution of nocturnal body temperatures, the modes appearing to reflect two distinct physiological states. At ambient temperatures <17°C, body temperature conformed to the higher level (Fig. 3A), although measured at night. Those data raise the possibility that the unusually high rate of metabolism in thermoneutrality in this toucan is not representative of standard conditions, and therefore is not basal (see McNab 1997). Clearly, more work on the energetics of that species is required to clarify its characteristics. Secondly, the high rates of metabolism of *Ramphastos toco* measured in the smaller chamber may have reflected anxiety produced by the enclosure of those large toucans into a small space. Those concerns have led to the exclusion of the measurements on *S. maculirostris* and the small chamber values for *R. toco* in the following analyses.

Basal rate of metabolism.—Data on basal rate, climate, food habits, and family affiliation in seven species of toucans, *Trachyphonus*, and other members of the order Piciformes, namely woodpeckers, as well as tropical nonpasserine frugivores, including mousebirds and the hornbill, are summarized in Table 1. The basal metabolic rates of toucans were similar to, or somewhat below, those predicted by the Aschoff-Pohl curve for birds other than passerines and well below the Reynolds-Lee curve (Fig. 6). The greatest reduction in basal rate compared with standard curves was found in *Trachyphonus*, which is only 71% of the value expected from mass by the Aschoff-Pohl curve. Blyth's Hornbill, which is frugivorous, and mousebirds (*Urocolius macrourus*, *Colius striatus*, and

TABLE 1. The standard energetics of piciform and frugivorous nonpasserine birds.

Species	Body mass (g)	Basal rate of metabolism ($cm^3O_2h^{-1}$)	Minimal thermal conductance (cm^3O_2 $h^{-1}°C^{-1}$)	Climate[a]	Food habits[b]	Source
			Lybiidae			
Trachyphonus darnaudii	36.6	39.2	5.3	Arid	Omniv	This study
			Ramphastidae			
Aulacorhynchus sulcatus	131.7	121.6	7.8	Trop	Fruit	This study
Baillonius bailloni	133.0	126.0	9.2	Trop	Fruit	This study
Aulacorhynchus prasinus	174.7	149.2	8.9	Trop	Fruit	This study
Pteroglossus aracari	200.7	159.4	17.9	Trop/sub	Fruit	This study
Ramphastos dicolorus	328.9	226.6	13.4	Sub	Fruit	This study
Ramphastos tucanus	420.3	306.4	18.9	Trop	Fruit/car	This study
Ramphastos toco	582.0	434.9	19.8	Trop/sub	Fruit/car	This study
			Picidae			
Jynx torquillo	31.8	64.2	—	Temp	Insect	Kendeigh et al. 1977
Melanerpes formicivorous	73.1	128.7	—	Temp	Acorn	Weathers et al. 1990
Dendrocopus major	98.0	160.0	—	Temp	Insect	Kendeigh et al. 1977
			Bucerotidae			
Aceros plicatus	1,781.6	814.3	37.4	Trop	Fruit	This study
			Coliidae			
Urocolius macrourus	51.3	51.3	5.4	Trop	Fruit/leaves	Prinzinger 1988
Colius striatus	52.5	57.8	4.7	Trop/sub	Fruit/leaves	Bartholomew and Trost 1970
Colius castanotus	69.0	82.1	7.7	Trop	Fruit/leaves	Prinzinger et al. 1981

[a] trop = tropical; trop/sub = tropical and subtropical; sub = subtropical; temp = temperate.

[b] omniv = omnivorous; fruit = frugivorous; fruit/car = frugivorous and carnivorous; insect = insectivorous; acorn = acorn and insectivorous; fruit/leaves = fruit and leaves.

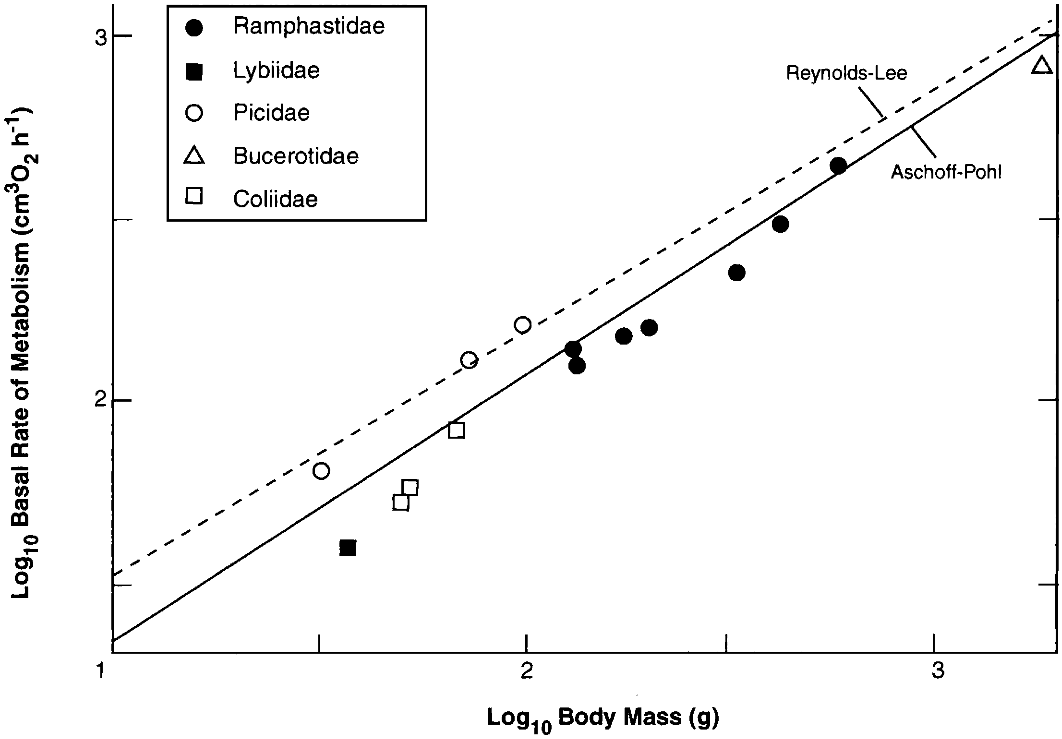

FIG. 6. $\log_{10}$ total basal rate of metabolism as a function of $\log_{10}$ body mass in frugivorous nonpasserine birds. The standard curve for birds other than passerines (Aschoff and Pohl 1970) and for all birds (Reynolds and Lee 1996) are included. Data from Table 1 and references therein.

C. castanotus), which feed on fruit and leaves, had basal rates (Bartholomew and Trost 1970, Prinzinger et al. 1981, Prinzinger 1988), compared to the Aschoff-Pohl curve, similar to, or below, those found in toucans (Fig. 6). The few data available on woodpeckers, namely two European species (*Jynx torquillo* [Wryneck] and *Dendrocopos major* [Great Spotted Woodpecker]) and the North American Acorn Woodpecker (*Melanerpes formicivorous*), indicated higher basal rates than expected from mass (Kendeigh et al. 1977, Weathers et al. 1990) and much higher residuals than found in toucans and mousebirds (Fig. 6).

In an analysis of covariance, $\log_{10}$ basal rate was not correlated with climate ($P = 0.57$), food habits ($P = 0.99$), and family affiliation ($P = 0.30$) when entered together with $\log_{10}$ body mass. However, when food habits were entered alone with mass, $\log_{10}$ basal rate was correlated both with $\log_{10}$ body mass ($F = 552.83$, df = 1 and 8, $P \leq 0.0001$) and food habits ($F = 21.59$, df = 5 and 8, $P = 0.0002$; $R^2 = 0.995$). Species with omnivorous, frugivorous, or fruits mixed with other foods have indistinguishable basal rates, as do those with insectivorous and acorn-eating habits. Thus, when those categories were lumped into two categories, $\log_{10}$ basal rate was correlated with $\log_{10}$ body mass ($F = 1346.87$, df = 1 and 12, $P \leq 0.0001$) and food habits ($F = 82.93$, df = 2 and 12, $P \leq 0.0001$; $R^2 = 0.991$). Then, $\dot{V}_{O_2}$ (cm³ O_2h^{-1}) = $4.34\, f\, g^{0.786}$, where f is a dimensionless coefficient that represents food habits. In this analysis, fruit-eating nonpasserines (toucans, barbet, and hornbill) have basal rates that are 59% of those of acorn- and insect-eating species (woodpeckers), that is, $f = 1.00$ for insect and acorn-eaters and $f = 0.59$ for frugivores.

The analysis of avian frugivory can be expanded further by comparing energetics of toucans, barbet, and hornbill with frugivorous pigeons and doves (Columbidae) and flying foxes (Pteropodidae). Those data, expressed in mass-specific rates, are shown as a function of body mass in Figure 7. Notice that the data generally

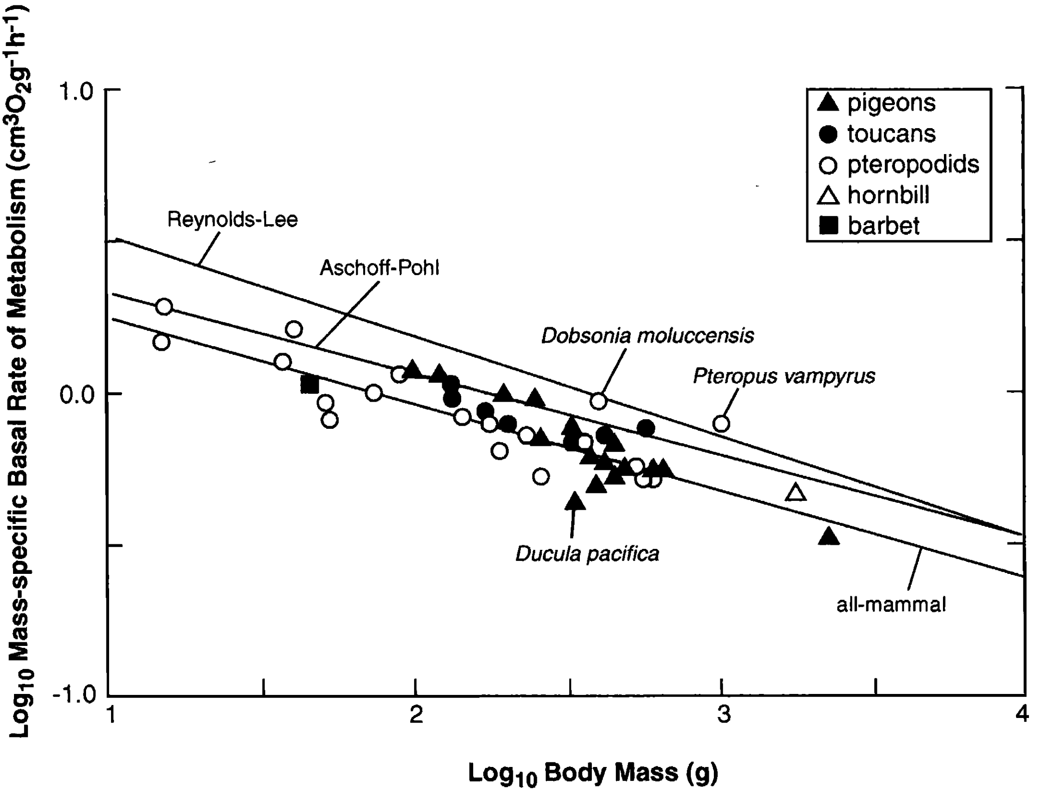

FIG. 7. Log_{10} mass-specific basal rate of metabolism as a function of log_{10} body mass in a barbet, toucans, a hornbill, fruit pigeons (McNab 2000), and flying foxes (McNab and Armstrong 2001, McNab and Bonaccorso 2001). Also indicated are the standard curves for nonpasserines (Aschoff and Pohl 1970), all birds (Reynolds and Lee 1996), and all mammals (McNab 1988a).

fall on top of each other. The highest residuals in basal rate are found in two flying foxes (*Dobsonia moluccensis* and *Pteropus vampyrus*), whereas the lowest residual is found in a fruit pigeon (*Ducula pacifica*)—that is, the highest basal rates are found in two mammals and the lowest in a bird. In other words, no clear differences exist in basal rates among frugivorous toucans, pigeons, and flying foxes (except for some small [<40 g] nectarivorous pteropodids that were not included because they are imprecise thermoregulators [Bonaccorso and McNab 1997, McNab and Bonaccorso 2001]). Nonpasserine frugivores thus have low basal rates, although the largest toucans tend to have slightly higher basal rates, possibly associated with an increased level of carnivory.

When climate is entered only with log_{10} body mass, log_{10} basal rate correlated with both factors ($F = 21.20$, df = 4 and 9, $P \leq 0.0001$, and $F = 1050.75$, df = 1 and 9, $P \leq 0.0001$, respectively; $R^2 = 0.993$). No difference was found between tropical, subtropical, subtropical–tropical, or arid distributed species. Therefore, climates were lumped into two categories, temperate and tropical. When climate categories were just two, log_{10} basal rate is correlated with log_{10} body mass ($F = 1346.87$, df = 1 and 12, $P \leq 0.0001$) and climate ($F = 82.93$, df = 1 and 1; $R^2 = 0.991$). Then, $\dot{V}_{O_2}$ ($cm^3O_2h^{-1}$) = $2.55\, c\, g^{0.786}$, where temperate species have $c = 1.70$ and tropical species $c = 1.00$. The difficulty with that conclusion is that food habits and climate in this sample are not independent: temperate species are insect- or acorn-eaters, whereas the tropical and subtropical species are frugivores. So, the high basal rate of temperate woodpeckers may simply reflect their insectivorous or acorn-eating habits. (In this context, measurements of energetics of fruit-eating, neotropical woodpeckers, such as some species of *Celeus* and *Melanerpes*, would be valuable.)

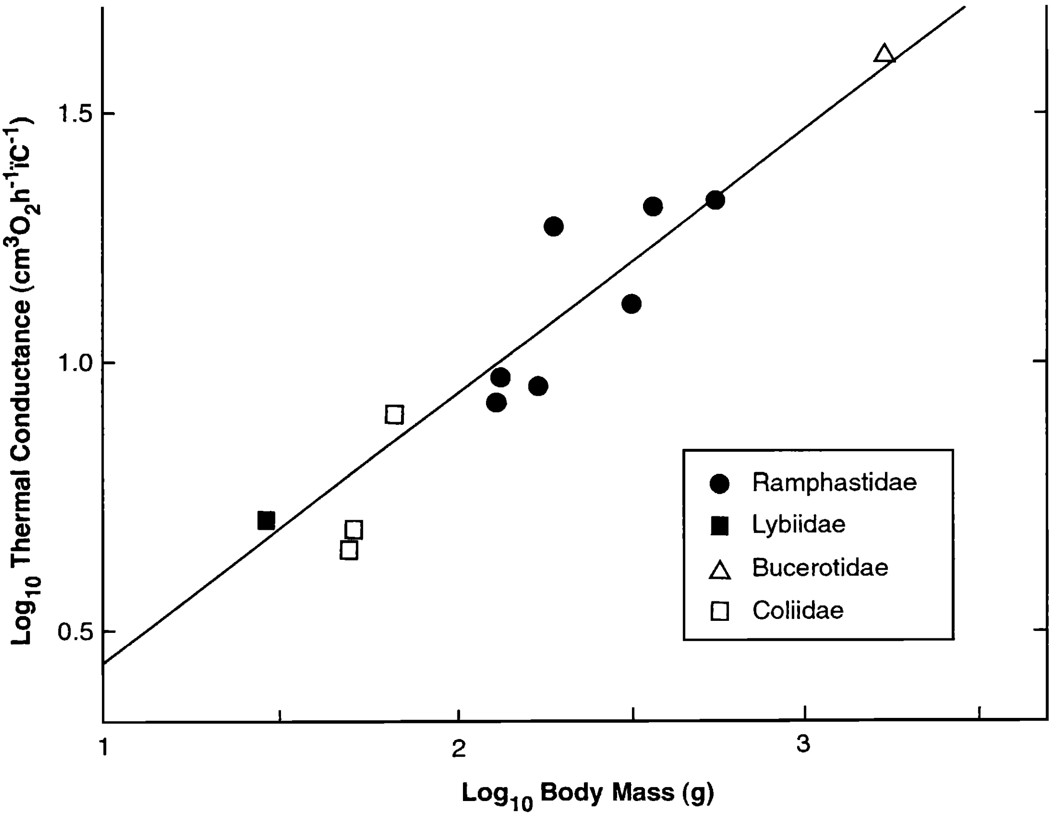

FIG. 8. Log_{10} total thermal conductance as a function of $\log_{10}$ body mass in frugivorous nonpasserine birds. The standard curve of Lasiewski et al. (1967) is indicated.

The parameters of avian energetics often are also correlated with phylogeny (Bennett and Harvey 1987), but whether ancestry limits performance is open to question; besides, no quality phylogeny exists for toucans (D. W. Steadman pers. comm.). In this study, $\log_{10}$ basal rate is correlated both with $\log_{10}$ body mass ($F = 354.45$; df = 1 and 9, $P \leq 0.0001$) and family affiliation ($F = 28.09$; df = 1 and 4, $P \leq 0.0001$, $R^2 = 0.995$), but only if climate and food habits are not included. As pointed out by Westoby et al. (1995), many factors interact to determine complex character states, such as basal rate of metabolism. For example, most toucans have masses between 130 and 400 g, are frugivorous, are tropical in distribution, and have low basal rates, as well as sharing a common ancestry, whereas studied woodpeckers are insect- or acorn-eating, are temperate in distribution, and have high basal rates. One cannot allocate those interacting character states exclusively to phylogeny as the causitive agent, as is usually done in the so-called "comparative method," any more than one can allocate them exclusively to "behavior" or "ecology." How to partition interactions to various causitive agents is presently unclear and may be impossible. Besides, is it possible to conceive of a toucan having a low basal rate because of ancestry if the low rate is ecologically unacceptable? If not, presence of a low basal rate in toucans is more likely related to frugivory (and tropical distribution) of toucans. The allocation of responsibility for a low basal rate to "phylogeny" needs the demonstration of a functional association of that character state with the evolution of some distinctive toucan property (e.g. the evolution of high basal rates in mammals was associated with evolution of a eutherian form of reproduction; McNab 1986, Lillegraven et al. 1987).

Minimal thermal conductance.—The only factor influencing $\log_{10}$ minimal thermal conductance among seven toucans, a barbet, a hornbill, and three tropical mousebirds was $\log_{10}$

body mass ($F = 116.04$, df = 1 and 10, $P \leq 0.0001$; $R^2 = 0.921$; Fig. 8).

A remarkable observation on conductance was that the largest toucan, *R. toco*, had a very low thermal conductance at low environmental temperatures, thereby reducing heat loss and rate of metabolism without decreasing core body temperature. A similar reduction in rate of metabolism at low environmental temperatures has been described in some tropical mammals of intermediate size, namely a tree-kangaroo (*Dendrolagus matschiei*), the red panda (*Ailurus fulgens*), and several arboreal viverrids (McNab 1988b, 1995); it was explained due to an enhanced peripheral vasoconstriction. The effect of a small chamber, noticed here in the Toco Toucan, may be due to claustrophobic anxiety and the consequent occurrence of a high heart rate, high blood pressure, and absence of peripheral vasoconstriction. Failure to reduce rate of metabolism at low temperatures as a result of confinement in small chambers also has been reported in a lemur (McNab 1988b) and a viverrid (McNab 1995).

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